

NEW SILURIAN NEOTAXODONT BIVALVES FROM SOUTH WALES AND THEIR PHYLOGENETIC SIGNIFICANCE

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ABSTRACT. The arcoidean bivalves, *Trecanolia acincta* gen. et sp. nov. and *Uskardita mikraulax* gen. et sp. nov., are described from the Wenlock of South Wales. These bivalves are accommodated within the new family Frejidae, alongside the closely related Silurian genera *Freja* Liljedahl and *Alytodonta* Cope. The frejids are characterized by an amphidetic, chevron-shaped duplivincular ligament, and a ventrally diverging dental arrangement of pseudocardinals and pseudolaterals. The group provides further evidence that the superfamily Arcoidea evolved from an early Ordovician ancestor, such as *Catamarcaia* Sánchez and Babin. The frejids represent an early diversification of the arcoideans, previously unknown in the Palaeozoic.

THE subclass Neotaxodonta was proposed by Korobkov (1954) to distinguish the arcoid and limopsoid bivalves from the nuculoids. The two groups share a superficially similar taxodont dentition that had long caused them to be taxonomically linked, following an initial proposal by Douvillé (1912). The subclass Palaeotaxodonta, proposed by Korobkov (1954) for the nuculoids, was accepted in the bivalve volumes of the *Treatise* (Cox *et al.* 1969–71). However, the Neotaxodonta – which removed the superfamilies Arcoidea and Limopsoidea from the pteriomorphian bivalves – was not.

Taylor *et al.* (1969, 1973) argued that the shell microstructure of the superfamilies Arcoidea and Limopsoidea provided good grounds for separating them from other pteriomorphians, and Cope (1995) proposed that the Neotaxodonta be recognized as distinct from the Pteriomorphia. As removal of these two superfamilies from the Pteriomorphia, as a restricted order Arcoidea, left many former arcoids within the Pteriomorphia without ordinal status, Cope (1996) assigned these to the order Cyrtodontida.

The neotaxodonts have a well established Mesozoic to Recent history, but their Palaeozoic origin and subsequent diversification is contentious. Many previous phylogenetic schemes considered the cyrtodontid pteriomorphians as the probable ancestors of the arcoid neotaxodonts (e.g. Newell 1954, 1965; Cox 1960; Vogel 1962; Cox *et al.* 1969–71; Pojeta 1971, 1978; Waller 1978, 1990). This view was reinforced by the known fossil record, as rich Ordovician faunas of cyrtodonts were known, but the earliest undisputed arcoids were of Devonian age. Possible earlier forms included two poorly known Ordovician species referred to *Parallelodon*. Babin (1966) showed that *P. antiquus* Barrois, 1891 was based on a poorly preserved specimen and that Barrois' figures were highly interpretative. Furthermore, *Glyptarca primaeva* Hicks, 1873 (included in the *Treatise* within *Parallelodon*) was described by Carter (1971) and Cope (1996) as a palaeoheterodont. The earliest undoubted neotaxodont form included in the *Treatise* was therefore the Devonian *Parallelodon*. Recently this view has been challenged (Cope 1997a, 1997b).

Sánchez and Babin (1993) described the genus *Catamarcaia* from the Middle Arenig of Argentina (see Text-fig. 6). This genus combines continuous dentition (i.e. lacking an edentulous area on the hinge-plate) with a duplivincular ligament; they considered it as a pteriomorphian with palaeoheterodont affinities. However, Cope (1997a) concluded that the continuous dentition of *Catamarcaia* was not characteristic of Ordovician pteriomorphs, but was more typical of neotaxodonts. Furthermore, the dental arrangement of *Catamarcaia* is similar to that of the palaeo-

heterodont *Glyptarca*. This suggests that the neotaxodonts could have evolved directly from the palaeoheterodonts. Cope (1997b) carried these arguments further and figured a Silurian neotaxodont, *Alytodonta gibbosa*, showing characters intermediate between *Catamarcaia* and the Wenlock genus *Freja* Liljedahl, 1984.

Herein we describe two new genera of neotaxodonts from the Wenlock Series of South Wales and assess their phylogenetic implications.

SYSTEMATIC PALAEOLOGY

All linear measurements are given in millimetres (mm), measured with Vernier callipers under a binocular microscope. Abbreviations used for dimensions, angles and statistics are: α° = angle of obliquity, AL = anterior length, CH = cardinal area height, CL = cardinal area length, L = length, H = height, OL = oblique length, S.D. = standard deviation, U° = umbonal angle, UH = umbonal height, and W = width. The following abbreviations are used to describe preservation: I = internal, E = external, R = right, L = left, A = articulated, C = complete valve, P = slightly fragmented valve, F = fragment, X = recrystallized calcite shell; the letters are combined to describe the preservation of each specimen (e.g. an ILC is a complete internal mould of a left valve). The specimens are housed in the collections of the British Geological Survey, Keyworth (BGS).

Subclass NEOTAXODONTA Korobkov, 1954
Order ARCOIDA Stoliczka, 1871
Superfamily ARCOIDEA Lamarck, 1809
Family FREJIDAE fam. nov.

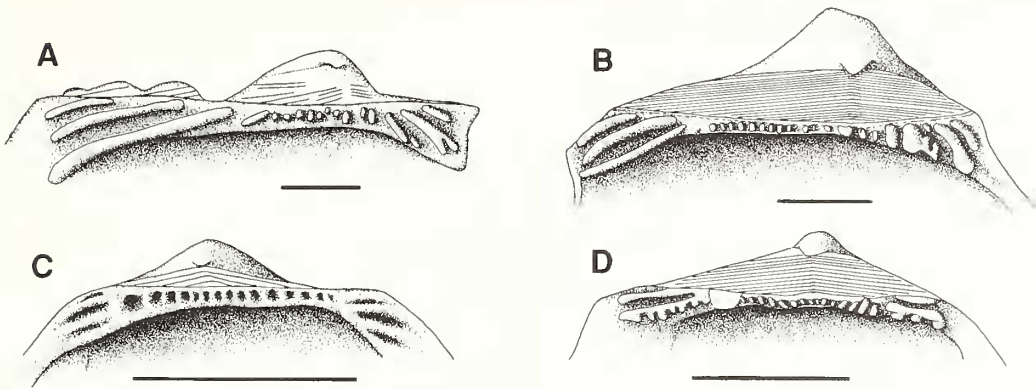
Type genus. *Freja* Liljedahl, 1984 (p. 36), here designated.

Diagnosis. Equivalved, subequilateral to inequilateral, moderately inflated arcoids, with a sub-orbicular to ovoid outline; ligament external, duplivincular, chevron-shaped and positioned on a cardinal area; hinge line straight; dentition of simple pseudocardinal teeth on the central hinge area, bounded anteriorly and posteriorly by pseudolaterals, elongated obliquely to hinge line; adductor muscle scars anisomyarian; external prosocon of concentric growth lines only.

Remarks. This new family is established to accommodate Silurian representatives of the superfamily Arcoidea. These include the genera *Freja* Liljedahl, 1984, *Alytodonta* Cope, 1997b, *Trecanolia* gen. nov. and *Uskardita* gen. nov. (Text-fig. 1). The frejids are characterized by a sub-circular to ovate outline and a straight hinge line. The dentition consists of a series of small, simple pseudocardinal teeth along the central area of the hinge plate, which are terminated by anterior and posterior pseudolateral teeth that are elongated at an oblique angle to the hinge line. The earlier genera, namely *Alytodonta* and *Uskardita*, have much shorter anterior pseudolaterals that are more oblique to the hinge line than later representatives. *Trecanolia* has more modified pseudolateral dentition; the undersides of the ventral teeth have cardinal denticles developing at irregular intervals. All four genera have a chevron-shaped duplivincular ligament between the hinge plate and the beak.

Liljedahl (1984, pp. 36–37) was unsure of the systematic position of *Freja* at the superfamily and family level. At that time, the newly described genus had a unique hinge construction and gross shell morphology. The prosocline outline, straight hinge line and anisomyarian adductors were typical in the cyrtodontoideans, yet the hinge plate and ligament closely resembled the Mesozoic and Cenozoic arcids. With the recent discovery of closely related genera from the Llandovery and Wenlock of Britain, it is possible to view the morphology of *Freja* as typical of this family of Silurian arcoids and it is herein considered as the type genus.

Cope (1997b, pp. 740–741) erected the new genus *Alytodonta*, which was based on a single specimen from the Lower Llandovery at Girvan, Ayrshire. *Alytodonta* displays the duplivincular



TEXT-FIG. 1. Hinge details of the four frejida genera. A, *Alytodonta gibbosa* Cope, 1997b; Natural History Museum L 49858; modified from Cope 1997b, text-fig. 4. B, *Uskardita mikraulax* gen. et sp. nov.; BGS GSM 22187. C, *Freja fecunda* Liljedahl, 1984; Geological Survey of Sweden Type 3367; modified from Liljedahl 1984, fig. 21. D, *Trecanolia acincta* gen. et sp. nov.; BGS DEX 2869. Scale bars represent 4 mm.

ligament, subovate outline and continuous dentition that characterize the Frejidae. In his description, Cope (1997b) placed *Alytodonta* within the family Parallelodontidae. However, this group contains predominantly Mesozoic and Cenozoic genera that have hinge plates, shell outlines and external prosopon that are easily distinguished from the Frejidae. The parallelodontids have a more inequilateral dental arrangement, chiefly consisting of short, oblique anterior teeth and very long posterior pseudolaterals that are almost parallel with the hinge line. Furthermore, their shells are usually antero-posteriorly elongated and ornamented with both concentric growth lines and radial ridges and gutters.

The family Frejidae cannot accommodate *Catamarcaia*, which displays a duplivincular ligament and a composite dentition of actinodontoid laterals and some small taxodont teeth (Sánchez 1995). The combination of these characters is unique to this bivalve and has resulted in previous uncertainty regarding its systematic position. It is clearly a neotaxodont but, as yet, cannot be readily accommodated in any existing family.

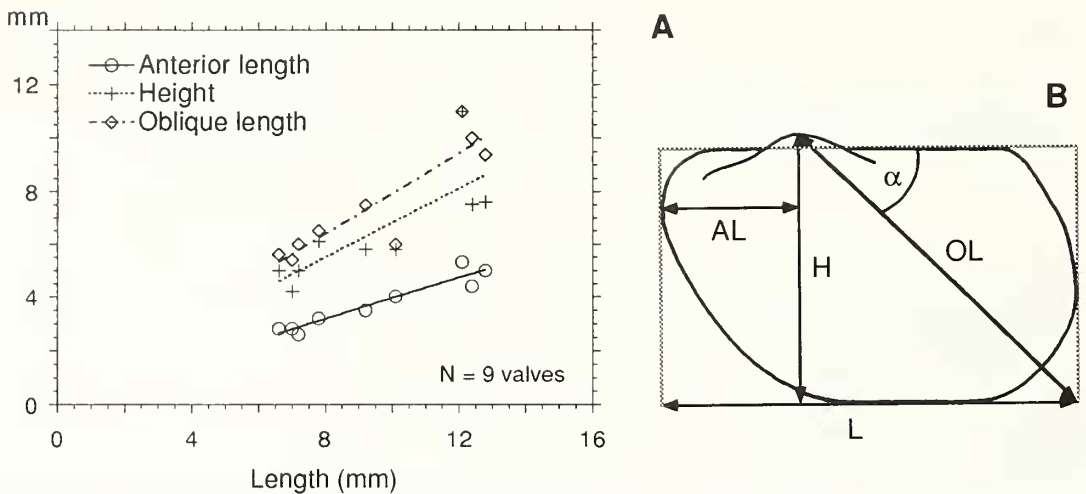
Stratigraphical range. Lower Llandovery to Upper Wenlock of Britain, Upper Wenlock of Gotland (Sweden), and possibly the Wenlock of Wisconsin, USA.

Genus TRECANOLIA gen. nov.

Derivation of name. From the Welsh *tre* (= settlement), and *canol* (= middle) – the Welsh equivalent of ‘Middleton’, an allusion to the type locality.

Type species. *Trecanolia acincta* sp. nov., by monotypy.

Diagnosis. Equivalved, inequilateral, moderately inflated, opisthocline, sub-orbicular to oblique shells with a narrow, straight hinge plate, gently rounded posterior and ventral margins and a narrow, strongly convex anterior extremity; umbones elevated above hinge line; beaks orthogyre. Dentition of 11–18 simple, cardinal teeth proximal to umbonal area, terminated by two short anterior pseudolaterals and two longer posterior pseudolaterals; both sets elongated normal to hinge plate; underside of ventral anterior pseudolateral has three to six cardinal denticles; ventral side of posterior pseudolaterals has up to seven taxodont denticles, juvenile specimens may lack the posterior denticles; subumbonal edentulous space present only in juveniles. Adductor scars anisomyarian; anterior adductor scar ovate and supported by shallow myophoric buttress;



TEXT-FIG. 2. A, bivariate scatter diagram of dimensions measured on *Trecanolia acincta* gen. sp. nov. B, angles and measurements taken on *T. acincta*.

posterior scar larger, but less deeply impressed. Ligament duplivincular and chevron-shaped, located between hinge and beak. External prosoxon unknown.

Remarks. *Trecanolia* is distinguished from other frejids by the oblique and posteriorly elongate shell shape and by the presence of large denticles on the underside of the ventral anterior and posterior pseudolaterals (Text-fig. 3). *Trecanolia* is most closely related to *Freja*; both genera have numerous cardinal teeth and pseudolaterals oriented normal to the hinge plate, similar anisomyarian adductors, and orthogyre beaks. However, *Freja* has an orbicular, subequilateral shell outline, a gently convex anterior margin, less elongate posterior pseudolaterals and lacks the unusual denticles. *Uskardita* is easily distinguished from *Trecanolia* by the large cardinal area, more conspicuous duplivincular ligament, oblique and shorter anterior cardinal teeth and the more upright umbo. *Alytodonta* is more distantly related, as the three posterior pseudolaterals are elongate and rather pteroid in appearance and the beaks are prosogyrate.

Trecanolia acincta gen. et sp. nov.

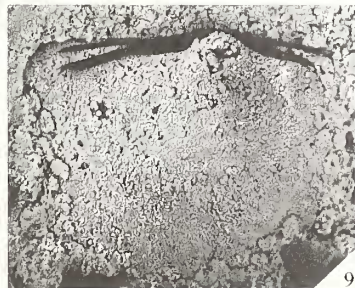
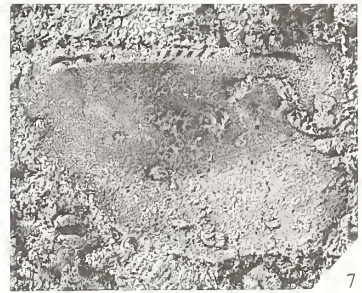
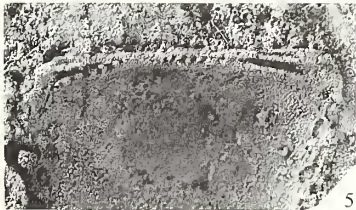
Plate 1, figures 1–10; Text-figures 2–3

v. 1978 Bivalve gen. et sp. nov.; Squirrel and White, pl. 3, figs 12–14
 (?) 1996 *Leiopteria* cf. *undata* (Hall, 1852); Watkins, fig. 2E.

Derivation of name. From the Latin *acinctus* (= well equipped); referring to the numerous teeth and denticles.

EXPLANATION OF PLATE I

Figs 1–10. *Trecanolia acincta* gen. et sp. nov.; overflow cut from the old lake in Middleton Hall Estate, near Middleton Hall Lodge, 2995 metres S68° W of Dryswlyn Station, Carmarthenshire; grid reference SN 5265 1880; probably Upper Wenlock. 1, BGS DEX 2869A, holotype; internal mould of left valve; $\times 5$. 2, latex cast of holotype; $\times 5$. 3–4, BGS DEX 2834B; internal mould of left valve and latex cast; $\times 7$. 5, 9, BGS DEX 2869B; hinge detail of latex cast and internal mould of right valve; $\times 6$. 6–7, BGS DEX 2843A; internal mould of right valve and latex cast; $\times 6$. 8, BGS DEX 2848; dorsal view of conjoined valves, internal mould; $\times 4$. 10, BGS DEX 2880; internal mould of left valve; $\times 5$.



Holotype. BGS DEX 2869A, a complete internal mould of a left valve. The specimen has been tectonically distorted resulting in a shortened antero-posterior axis. No undeformed specimens have been collected.

Paratypes. BGS DEX 2869B (ILC), BGS DEX 2823A (IRF), BGS DEX 2834A, B, C, D, E (IRC, ILC, IRF, ILC and IRP respectively), BGS DEX 2839A (ILC), BGS DEX 2841 and 2847A (ILF and ELF – part and counterpart), BGS DEX 2847B, C, D (IRF, ILF and IRP respectively), BGS DEX 2843A (IRP), BGS 2848 (IAF), DEX 2880A (ILP). All specimens are from the type locality and horizon.

Type locality and horizon. Overflow cut from old lake in Middleton Hall Estate, near Middleton Hall Lodge, 2995 metres S68° W of Dryswlyn Station, Carmarthenshire, west Wales; grid reference SN 5265 1880. Probably of late Wenlock age (Squirrel and White 1978).

Measurements

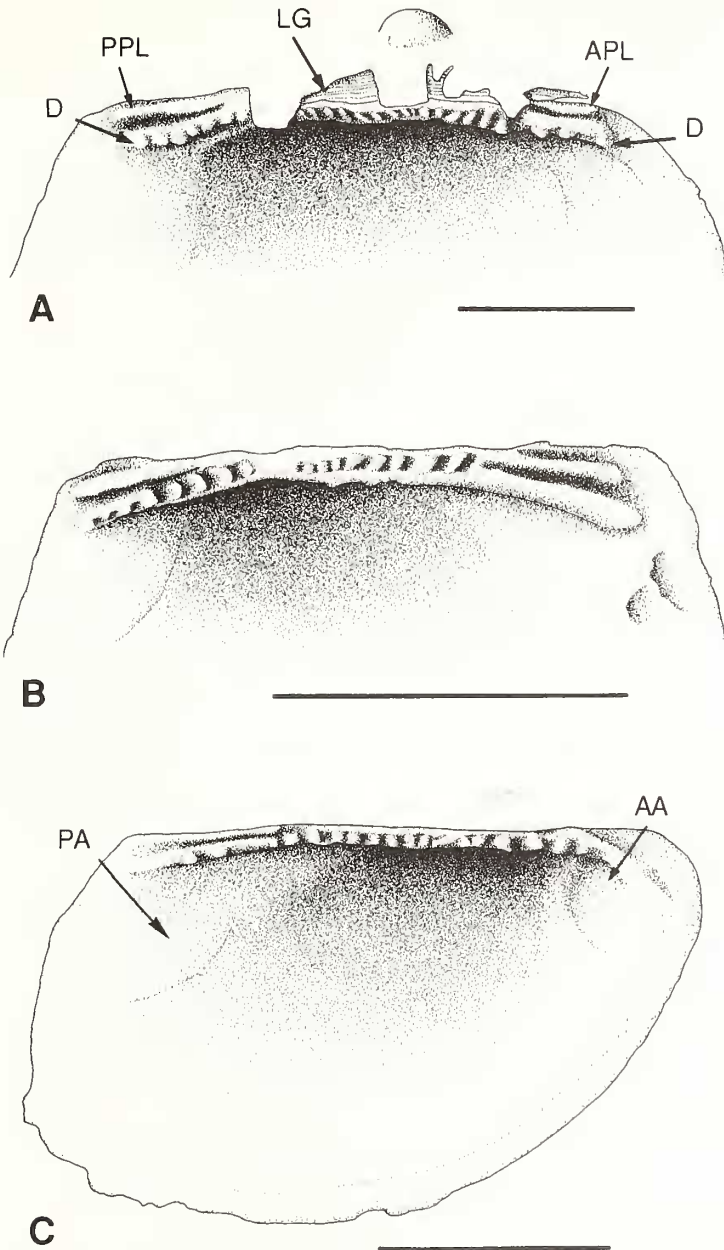
BGS DEX	AL	L	H	W	OL	AL/L	H/L	OL/L	U°	α°
2834A	5.0	12.8	7.6	2.0	9.4	0.39	0.59	0.73	117	45
2834B	3.5	9.2	5.8		7.5	0.38	0.63	0.82	117	47
2834D	4.4	12.4	7.5		10.0	0.35	0.60	0.81	115	44
2834E	2.6	7.2	5.0		6.0	0.36	0.69	0.83		
2839A	4.0	10.1	5.8	1.2	6.0	0.40	0.57	0.59	117	51
2843A	2.8	7.0	4.2		5.4	0.40	0.60	0.77	126	46
2869A	5.3	12.1	11.0	3.0	11.0	0.44	0.91	0.91	111	60
2869B	2.8	6.6	5.0		5.6	0.42	0.76	0.85	109	51
2880A	3.2	7.8	6.1		6.5	0.41	0.78	0.83	96	55
Min.	2.6	6.6	4.2	1.2	5.4	0.35	0.57	0.59	96	44
Max.	5.3	12.8	11.0	3.0	11.0	0.44	0.91	0.91	126	60
Mean	3.7	9.5	6.4	2.1	7.5	0.39	0.68	0.82	113.5	49.9
Median	3.5	9.2	5.8	2.0	6.5	0.40	0.63	0.82	116	49.0
S.D.	1.00	2.48	2.04	0.90	2.11	0.03	0.11	0.09	8.68	5.51

Diagnosis. As for genus.

Description. Small, inequilateral, equivalved, opisthocline, moderately inflated, oblique to sub-orbicular shells, with a straight dorsal margin, strongly convex anterodorsal margin, gently rounded anteroventral and ventral margin, slightly angulated posteroventral margin and a somewhat truncate and gently arcuate posterior. The maximum convexity is mid-height and just anterior of the mid-length of the shell. The umbones are situated in the anterior half of the shell, and are conspicuous and elevated above the hinge plate and interumbonal area. The beaks are small and orthogyrate.

BGS DEX	L × H	Cardinal teeth	Anterior denticles	Posterior denticles	Anterior pseudolaterals	Posterior pseudolaterals	Edentulous space?
2834A	97.28	~ 18	2	?	2	2	?
2834B	53.36	13	2–3	3	1	2	No*
2834E	36.00	7	2	~ 3	2	2	Yes (large)
2848 left	~ 96.00	17	3	?	?	?	Yes (small)
2848 right	~ 96.00	18	?	?	?	?	Yes (small)
2869A	133.10	15	3	7	2	2	No
2869B	33.00	12	4	0	2	2	Yes (small)

* Teeth in subumbonal area fused and poorly defined.



TEXT-FIG. 3. Hinge details of *Trecanolia acincta* gen. et sp. nov. The diagrams are *Camera lucida* drawings of latex casts. A, BGS DEX 2869A, holotype; left valve. B, BGS DEX 2869B; right valve. C, BGS DEX 2834B; left valve. AA = anterior adductor muscle scar; APL = anterior pseudolateral teeth; D = denticles; LG = duplivincular ligament and cardinal area; PA = posterior adductor muscle scar; PPL = posterior pseudolateral teeth. Scale bars represent 3 mm.

The dental arrangement consists of numerous cardinal teeth beneath the cardinal area, terminated by anterior and posterior pseudolaterals. The cardinal teeth are simple, peg-like, are elongated either perpendicular to the hinge line or radiate dorsally, and extend underneath the ligament area and between the anterior and

posterior adductor muscle scars; the number of teeth varies from seven to 12 in juveniles, and from 13 to 18 in more adult specimens; juveniles have a subumbonal edentulous area, but adults have a continuous series of teeth; intermediates display either a very small edentulous area or have small, poorly defined and fused teeth beneath the umbo. The anterior pseudolaterals usually number two and have two to four denticles on the underside of the ventral pseudolateral. The posterior pseudolaterals also number two, but are more elongate; denticles on the underside of the ventral pseudolateral are generally absent in smaller specimens, but number up to seven in the largest individual.

The adductor muscle scars are anisomyarian. The anterior adductor is small, ovate and well impressed; it is positioned ventral to the anteriormost part of the hinge. The posterior adductor is larger, but less well impressed and only visible in a few specimens; the scar is located ventral to the posterior pseudolateral teeth. No pedal muscle scars have been observed. A simple pallial line connects the adductor scars.

Only the holotype displays a chevron-shaped, external, duplivincular ligament on a small, triangular interumbonal or cardinal area, between the beak and the hinge plate.

The external prosopon consists of regularly spaced, commarginal growth lines.

Remarks. The holotype and paratypes were collected by Squirrel and White (1978, pl. 3, figs 12–14, illustrating specimens BGS DEX 2869A, 2869B and 2848) and named as 'Bivalve gen. et sp. nov.'. We have been unable to supplement this collection made in the 1960s, as the section was probably infilled soon after excavation. Within the studied collections, *T. acincta* accounts for approximately one-quarter of the abundant and diverse bivalve fauna. All of the specimens have been slightly deformed tectonically, so that biometric data and details of the shell outline are highly variable.

T. acincta may also occur in the Wenlock of Wisconsin. Watkins (1996) studied the palaeoecology of Silurian reef bivalves from the Racine Formation (mid Sheinwoodian to latest Wenlock in age). Four specimens from this sequence were named as *Leiopteria* cf. *undata* (Hall, 1852), but display some characters that are diagnostic of *T. acincta* (see Watkins 1996, fig. 2E). Denticles are visible beneath the dorsal anterior pseudolateral tooth, whilst the posterior pseudolateral is rather elongate. *L.* cf. *undata* also has a similar shell outline and umbonal area to *T. acincta*. Watkins commented that *L.* cf. *undata* was nearly equivalved (the equivalved condition is diagnostic for the Frejidae but not the Pterineidae), which suggests that this bivalve is not a *Leiopteria* nor indeed any other pterioidean. However, it is uncertain whether these specimens are Laurentian examples of *T. acincta*. This can only be established after examination of the material.

The dental arrangement displays a transition from juvenile to adult stages in this small population. The juvenile shells lack the subumbonal cardinal teeth (e.g. BGS DEX 2869B; Text-fig. 3B) and have either few or no denticles on the underside of the ventral posterior pseudolateral. However, a specimen (BGS DEX 2834B; Text-fig. 3C) transitional between the juvenile and adult stages has fused, poorly defined subumbonal teeth in a position corresponding with the edentulous space in smaller specimens. The largest valve known (BGS DEX 2869A; Text-fig. 3A), which probably represents the final ontogenetic stage, has a complete series of cardinal teeth and seven posterior denticles.

Genus USKARDITA gen. nov.

Derivation of name. The combination of Usk (a south-east Wales town located near the type locality) and *cardita* (Spanish for a small vessel, referring to a mollusc).

Type species. *Uskardita mikraulax* sp. nov., by monotypy.

Diagnosis. Inequilateral, equivalved, sub-orbicular, opisthocline, moderately inflated valves, with elevated, narrow, conspicuous umbo and weakly prosogyrate beaks; cardinal area large, uniconvex lens-shaped, with chevron patterned, external duplivincular ligament; hinge line straight; dentition of approximately 18 cardinal teeth, terminated by three ventrally divergent posterior pseudolaterals and two arcuate, ventrally divergent cardinal teeth; external prosopon of numerous, regular concentric growth lines.

TABLE 1. Comparison of the diagnostic characters of the genera *Alytodonta*, *Uskardita* and *Freja*.

	<i>Alytodonta</i>	<i>Uskardita</i>	<i>Freja</i>
Shell outline	Sub-orbicular	Sub-orbicular to ovate	Sub-orbicular to ovate
Umbones	Low	Elevated and erect	Low
Beaks	Prosogyrate	Weakly prosogyrate	Orthogyrate
Cardinal area	Small, but elongate	Large and uniconvex	Small and triangular
Ligament	Duplivincular, amphidetic with several furrows	Duplivincular, chevron shaped, several furrows	Duplivincular, chevron shaped, furrows very numerous
Pseudocardinals	11, subumbonal, diverge ventrally	Approximately 18, occupy most of hinge, normal to hinge line	13 in holotype, occupy centre of hinge plate, normal to hinge line
Anterior pseudolaterals	Five, of which two are small and one ventrally bifurcates, diverge ventrally	Two, small, arcuate, diverge ventrally	Three, straight, radiate ventrally but at a very low angle
Posterior pseudolaterals	Three, elongate, decrease in length dorsally, diverge ventrally	Three, short, decrease in length dorsally, diverge ventrally	Three, short, central tooth most elongate, almost parallel with hinge line
Musculature	Anisomyarian adductors plus ?posterior pedal retractor	Unknown	Anisomyarian adductors plus posterior byssal/pedal retractor, gill attachment site and visceral muscle scars
External prosoxon	Uncertain	Conspicuous commarginal growth lines	Faint commarginal growth lines
Age	Early Llandovery	? Sheinwoodian, early Wenlock	Late Wenlock

Remarks. *Uskardita* is known from only seven specimens, but displays characters that warrant the erection of a new genus. *Uskardita* is closely related to both *Alytodonta* and *Freja*, and is most probably an evolutionary intermediate between the two genera. The shell characters are compared in Table 1.

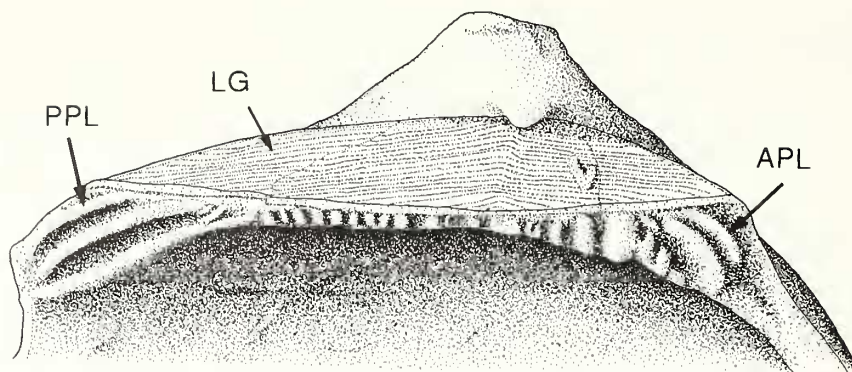
Stratigraphical range. 'Wenlock Shale', Sheinwoodian, of south-east Wales.

Uskardita mikraulax gen. et sp. nov.

Text-figures 4-5

Derivation of name. From the Greek adjective *mikraulax* (= small furrows), referring to the numerous ligament furrows on the cardinal area.

Holotype. BGS GSM 22187, a left valve with a fragmented ventral margin, preserved as recrystallized calcite.



TEXT-FIG. 4. *Uskardita mikraulax* gen. et sp. nov.; holotype, BGS GSM 22187; hinge detail of a left valve. APL = anterior pseudolateral teeth; LG = duplivincular ligament positioned on cardinal area; PPL = posterior pseudolateral teeth.

Paratypes. BGS GSM 21956 (XRP), 22029 (XRF), 22183 (XAP), 22184 (IRC), 22185 (XRC) and 22186 (XRP); all assumed to be from the same locality as the holotype.

Type horizon and locality. 'Wenlock Shale' exposed at Craig y Garcy, on the southern banks of the River Usk, 2 km north-west of Usk, Monmouthshire (grid reference SO 360 024).

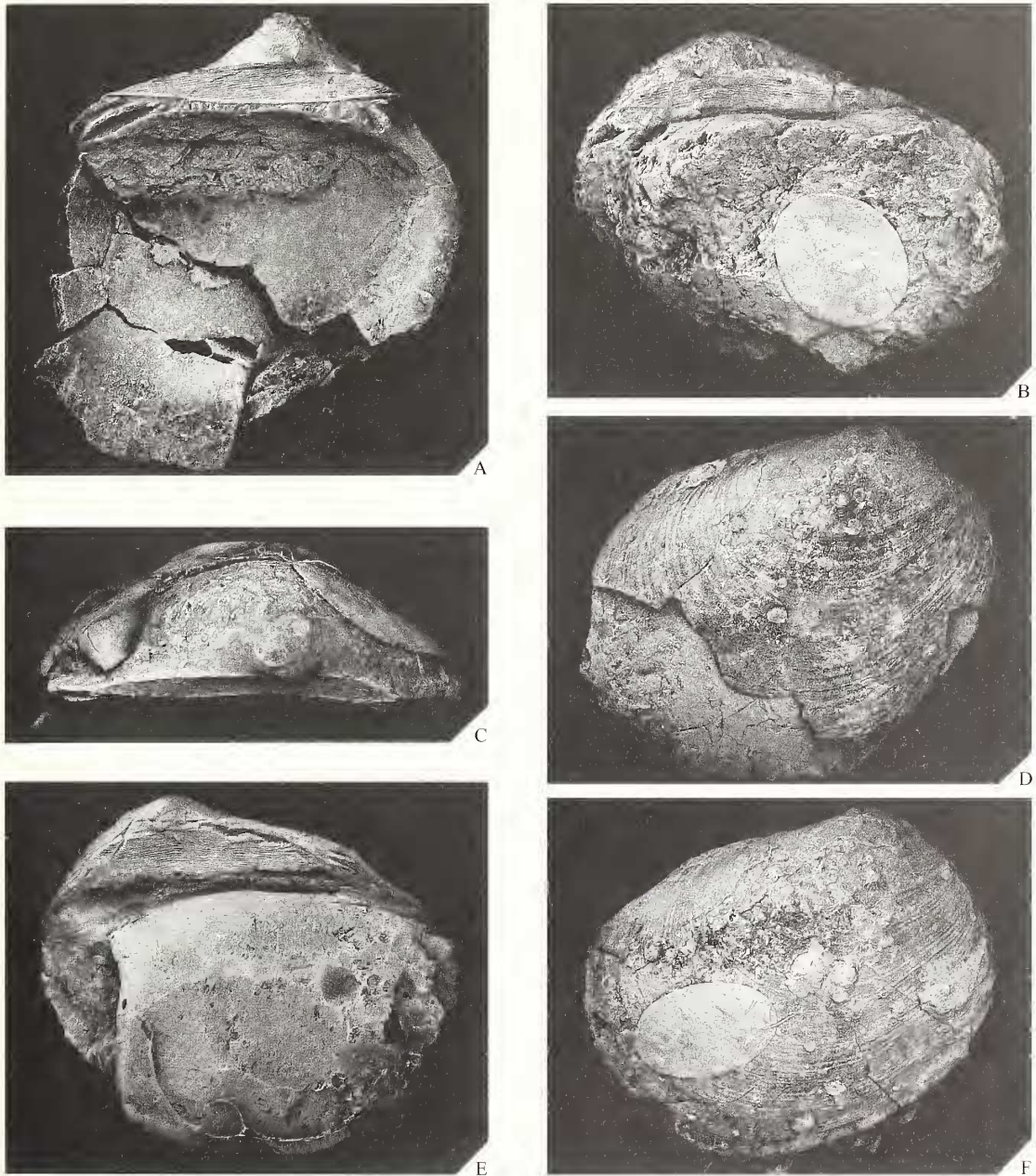
Measurements

BGS GSM	AL	L	H	W	OL	CL	CH	UH	AL/L	H/L	OL/L	H/ 2 × W	U°	α°
21956	9.5	25.1	~ 24.4	7.5	~ 24.4	~ 16.0	~ 2.5		0.38	0.97	0.97	1.63	132	57
22185	10.3	29.1	25.6	8.2	27.1	~ 18.0	3.0	2.8	0.35	0.88	0.93	1.56	130	54
22186	~ 7.0	~ 23.7	~ 20.9	6.9	~ 23.9	~ 15.0	~ 2.3	~ 2.0	0.29	0.87	1.00	1.51	125	54
22187	8.1	~ 23.7	24.5	~ 7.9	~ 23.0	15.0	2.4	2.5	0.34	1.03	0.97	1.55	97	60

Diagnosis. As for genus.

Description. Inequilateral, equivalved, opisthocline, moderately inflated, medium sized, sub-orbicular to ovate shells with a straight hinge line and gently convex anterior, posterior and ventral margins; the total length is slightly less than the height and oblique length (mean H/L = 0.94; mean OL/L = 0.97); the shell outline is only moderately oblique (mean α° = 56.3); maximum convexity is positioned approximately mid-height and mid-length. The umbones are one-third of the total length from the anterior margin (AL/L averages 0.34) and are conspicuous and elevated above both the cardinal area and the hinge plate; the beaks are weakly prosogyrate and poorly defined.

The dentition consists of pseudocardinal and pseudolateral teeth; the teeth and sockets extend over the entire hinge plate without edentulous spaces. The holotype has 18 small pseudocardinals on the narrow, central portion of the hinge plate which increase in size from the subumbonal area to the anterior; the large anteriormost pseudocardinal consists of three fused small teeth, adjacent to the anterior pseudolaterals. Two small, gently arcuate anterior pseudolaterals are located at the anterior extremity of the hinge plate; the posterior of the two is larger and thicker. Three elongate posterior pseudolaterals also radiate ventrally; the central and posterodorsal teeth are convex when viewed from the posterodorsal direction, whilst the anteroventral tooth is straight to slightly concave.



TEXT-FIG. 5. *Uskardita mikraulax* gen. et sp. nov.; Wenlock Shale, Craig y Garcyd, on the south bank of River Usk, 2 km north-west of Usk, Monmouthshire; grid reference SO 360024. A, BGS GSM 22187, holotype; interior of left valve preserved as calcite; $\times 2.5$. B, BGS GSM 22186; right valve displaying cardinal area; $\times 2.5$. C, dorsal view of holotype; $\times 2.5$. D, BGS GSM 22186; exterior view; $\times 2.5$. E-F, BGS GSM 22185; interior and exterior view of a right valve; $\times 2$.

A large, uniconvex lens-shaped cardinal or interumbonal area is situated between the hinge plate and the beak, which supports an external, amphidetic duplivincular ligament; the ligament covers the entire cardinal area and consists of numerous chevron-shaped furrows for the insertion of the ligament lamellar layers; the apices of the chevrons are located slightly posterior to the beaks. Approximately 20 furrows have been measured on the holotype (22 on BGS GSM 22185 and 13 on BGS GSM 22186).

The shell exterior is ornamented with regularly spaced, commarginal growth lines. Muscle scars are not preserved.

Remarks. It is assumed that all the specimens described were collected from a single locality within the 'Wenlock Shale', exposed at Craig y Garcyd on the River Usk, Monmouthshire. The labels that accompany the material either describe the locality simply as 'Usk' or 'Craig y Garcyd, Usk'. The recrystallized calcite preservation of brachiopods, trilobites and a single palaeotaxodont bivalve collected from the 'Wenlock Shale' at Craig y Garcyd (stored within the National Museum of Wales) help to confirm this site as the type locality.

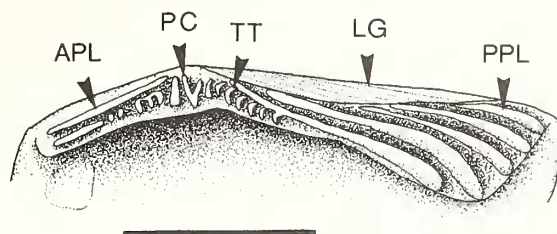
PHYLOGENY

The description of the bivalve genus *Catamarcaia* by Sánchez and Babin (1993, 1994: type species *C. chaschuilensis* Aceñolaza and Toselli, 1977) from the Middle Arenig of Argentina, has resulted in a revision of the early evolutionary history of the Arcoidea (characters summarized in Text-fig. 6). It is apparent that *Catamarcaia* is an innovative genus. Cope (1997a) proposed that a hypothetical ancestral arcoidean evolved from a *Glyptarca*-like palaeoheterodont during the Tremadoc with the appearance of a primitive duplivincular ligament and arcoidean dental arrangement. With minor modification of the dentition and ligament this gave rise both to *Catamarcaia* and, after the loss of the subumbonal dentition and shortening of the hinge-plate, to an early cyrtodontoidean lineage. This conclusion suggests that the Arcoidea (Neotaxodonta) appeared before the cyrtodontoidean pteriomorphs and conflicts with earlier phylogenetic schemes. Neotaxodonts are unknown from the middle or upper Ordovician; this is unsurprising if one considers that the arcoids were extremely rare and occupied a near-shore shelf environment. Both of the new South Wales genera are from localities very close to the shoreline of Pretannia, whilst *Alytodonta* also occurred in another close inshore situation at Girvan. The preservation potential of inshore facies is extremely low, resulting in a depleted fossil record.

In addition to *Trecanolia* and *Uskardita*, two other arcoid genera are known from the Silurian. *Freja fecunda* Liljedahl, 1984 was the first to be described. *Alytodonta gibbosa* Cope (1997b, pp. 739–741, pl. 4, figs 1, 5, 8) was originally described as a *Cyrtodonta* by Hind (1910), but Liljedahl (1984) showed that its continuous dentition precluded such an assignment. He concluded (1984, fig. 16) that both '*C.* *gibbosa* and *Freja fecunda* were closely related and shared a radical arcoid ancestor. Furthermore, Liljedahl stated that the radical arcoid descended from an 'actinodont' and was the ancestor of the Cyrtodontoidea. This view was followed by Amler (1989).

With the discovery of *Catamarcaia*, Liljedahl's hypothesis is probably in accordance with the fossil evidence. The rapid development of the duplivincular ligament from the hypothetical ancestor of *Catamarcaia*, postulated by Sánchez (1995, p. 344), may have continued during the Ordovician. If the cardinal area and opisthodetic duplivincular ligament of *Catamarcaia* began to extend towards the anterior, an amphidetic, chevron-shaped duplivincular ligament could have evolved – as seen in Silurian arcoideans. Thomas (1978) and Morris (1979) commented that the chevron-shaped arcoid ligament evolved from the cyrtodontids and early Ambonychioidea. Such a scheme must be questioned if one compares the ligaments of *Catamarcaia* and a typical lower Ordovician cyrtodontid, such as *Cyrtodonta saffordi* (Hall, 1859). Both ligament types are apparently composed of alternating lamellar and fibrous layers to the posterior of the umbones. However, the layers in *Cyrtodonta saffordi* are parallel to the hinge axis and at no point intersect the dorsal hinge margin, whereas in *Catamarcaia* the layers radiate and diverge ventrally so that they terminate on the hinge margin. It is suggested that the chevron-shaped ligament seen in the Silurian frejids is more closely related to the *Catamarcaia* ligament than to the cyrtodontid ligament. If it is assumed that the latter

TEXT-FIG. 6. Simplified sketch of the hinge of *Catamarcaia*, modified from Sánchez 1995, figure 1. APL = anterior pseudo-lateral tooth; LG = duplivoicular ligament; PC = pseudocardinal teeth; PPL = posterior pseudolateral teeth; TT = taxodont teeth. Scale bar represents 6 mm.



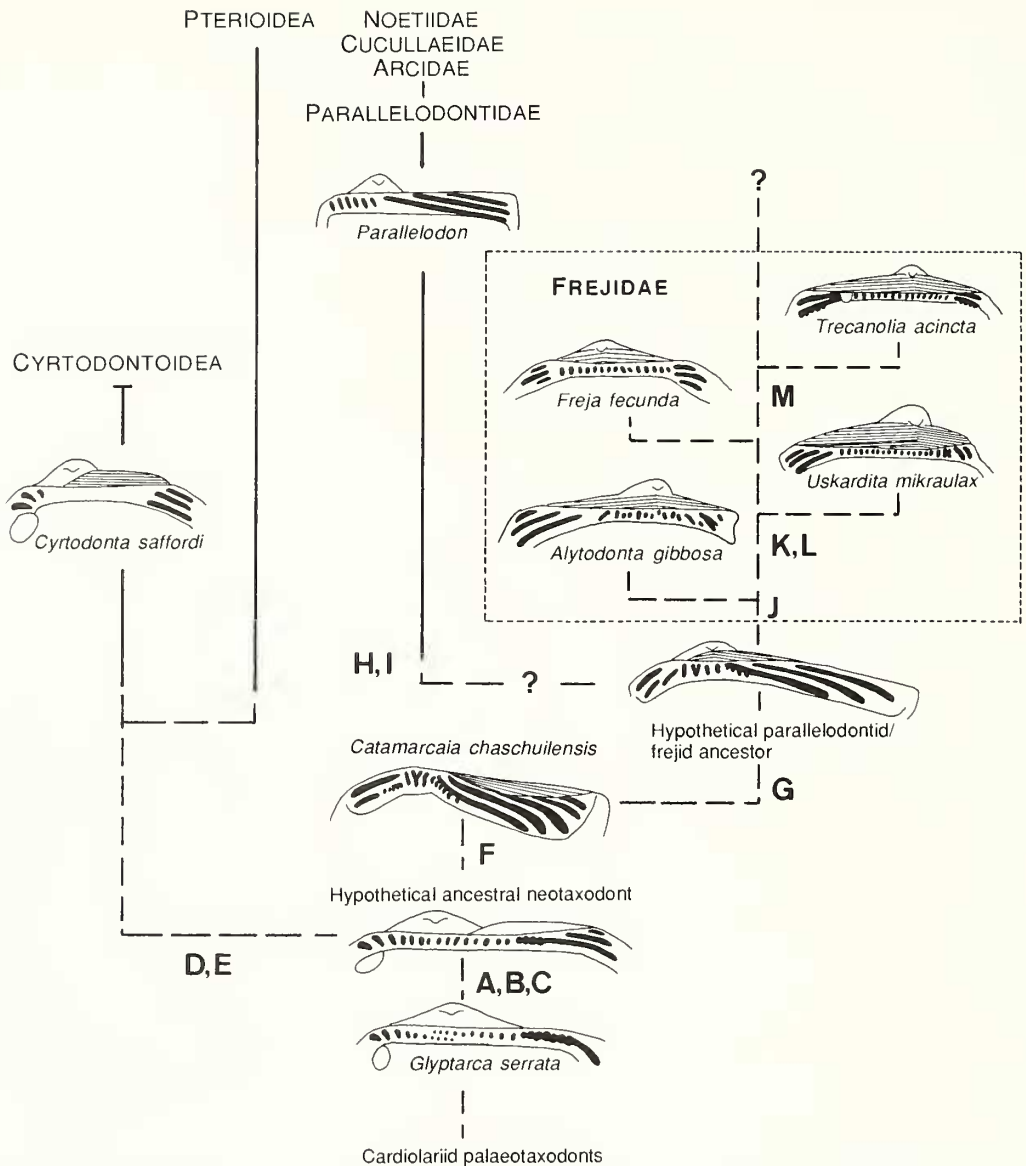
is more primitive, the fact that the earliest cyrtodontids are from the upper Tremadoc (Pojeta and Gilbert-Tomlinson 1977; Shergold *et al.* 1991) and thus pre-date *Catamarcaia*, indicates that they evolved earlier and feasibly from the hypothetical radical arcoïd proposed by Liljedahl (1984) and Cope (1997a). The chevron-shaped ligament may have arisen through anterior extension of the opisthodontic half-chevron resulting in another ventrally divergent half-chevron in front of the umbones. An amphidetic full chevron, as seen in the Frejidae, may have arisen subsequently.

The phylogeny of the arcoïdean dentition has been discussed by many authors (e.g. Stanley 1972; Pojeta 1978; Thomas 1978; Sánchez 1995). Prior to the recent work of Cope (1997a, 1997b) it was believed that the arcoïdean dental arrangement evolved from the cyrtodontids by the loss of the subumbonal edentulous space. However, the early arcoïdean *Catamarcaia* displays a dental arrangement sharing more affinities with *Glyptarca* and the early cycloconchids than the cyrtodontids (Cope 1997a, 1997b). This again conflicts with the contention that the cyrtodontids are more primitive than the arcoïdeans. If the cyrtodontids were ancestral to the arcoïdeans and evolved directly from a *Glyptarca*-like or an 'actinodont' ancestor (as proposed by Pojeta 1978; Thomas 1978; Morris 1979), this would require the loss of the subumbonal dentition, followed by the infilling of the resulting lacuna to produce an arcoïdean hinge (Cope 1997a, p. 128). Cope (1997a) remarked that such a scheme was not parsimonious and that a phylogeny whereby the arcoïdeans evolved from an ancestor with a continuous dentition was more likely. He also concluded that a hypothetical ancestral arcoïd with cardinals and posterior laterals and a newly evolved duplivoicular ligament gave rise to both the Cyrtodontidae and a *Catamarcaia*-like bivalve during the Tremadoc.

Knowledge of Lower Palaeozoic bivalve shell microstructure is very limited and extrapolating Ordovician and Silurian bivalve phylogeny using shell microstructural details of younger material must be treated with caution. Cope (1997b, pp. 727–733, text-fig. 1) has fully reviewed the early evolution of the shell microstructure. It was concluded that a parent aragonite (prismatic/crossed-lamellar/complex crossed-lamellar) arcoïdean shell microstructure probably descended directly from the aragonitic prismato-nacreous palaeoheterodont shell, rather than a calcitic outer layered shell (that probably characterized the early cyrtodontids, pteriods and ambonychioids). Furthermore, as each of these groups is tentatively considered to have had crossed-lamellar middle and complex crossed-lamellar inner shell layers, the most parsimonious phylogeny would dictate that the cyrtodontids evolved from the neotaxodonts with the development of an outer calcitic layer (Cope 1997a, 1997b).

Previous interpretations regarding the subsequent evolution of the Arcoïdea during the remainder of the Palaeozoic have been somewhat confused because the Arcoïdea were considered to have evolved directly from the cyrtodontids. As a consequence, malacologists tried to compare possible 'arcoïdean descendants' with the cyrtodontid dentition. Further confusion resulted from lack of knowledge of some early Ordovician putative *Parallelodon* (as discussed above).

The fossil record cannot yet confirm that the earliest parallelodontids were more closely related to a *Catamarcaia*-like bivalve than the frejids. Indeed, both groups can be conveniently linked with a *Catamarcaia*-like ancestor (Text-fig. 7). The earliest known frejid, *Alytodonta gibbosa* Cope, 1997b (from the Lower Llandovery of Ayrshire), has a continuous series of ventrally diverging pseudocardinal and pseudolateral teeth and an amphidetic, slightly chevron-shaped duplivoicular ligament. The subumbonal dentition is reminiscent of the bifurcating subumbonal pseudocardinals and the taxodont teeth seen in *Catamarcaia*. In addition, *Alytodonta* has three posterior



TEXT-FIG. 7. The origin and early evolutionary history of the order Arcoida: a possible phylogenetic scheme. Unbroken lines are based on fossil evidence, broken lines are hypothetical. The four representatives of the Frejidae are highlighted. The scheme is based on the following characters: A = loss of subumbonal dental overlap; B = appearance of an opisthodontic preduplivincular ligament; C = origin of a crossed-lamellar middle layer and complex-crossed-lamellar inner shell layer; D = loss of subumbonal dentition; E = origin of a prismatic calcite outer shell layer; F = appearance of an opisthodontic duplivincular ligament; G = development of an amphidetic duplivincular ligament; H = anteriorwards movement of umbones; I = rotation of anterior teeth to a ventrally convergent position; J = increase in number of pseudocardinals; K = further increase in pseudocardinals and reduction in pseudolateral teeth length; L = enlargement of cardinal area and duplivincular ligament; M = development of denticles.

pseudolaterals that resemble the five seen in *Catamarcaia*. A hypothetical intermediate between the first frejoid and the Arenig arcoid would probably display a half chevron-shaped ligament approaching the amphidetic state. The taxodont series seen in *Catamarcaia* may have then separated from the posteriorly migrating posterior pseudolaterals and the anterior pseudocardinals probably rotated anticlockwise.

Between the Lower Llandovery and the Lower Wenlock, evidence for further evolution within the Frejidae is provided by *Uskardita mikraulax*. This genus has a much enlarged cardinal area with numerous lamellar and fibrous ligament layer alternations (preserved as furrows) displaying conspicuous chevrons. *Uskardita* is the first arcoidean known with a chevron-shaped duplivincular ligament that is comparable to that of some of the Mesozoic to Recent Arcidae, Parallelodontidae and Cucullaeidae. The evolutionary significance of the large number of alternating lamellae and fibrous layers is unclear. Experimental work by Thomas (1976) on recent arcoids suggested that the rapid transverse growth of the ligament (as seen in *Uskardita*) results in numerous alternations of fibrous and lamellar layers, widely separated umbones and highly divergent cardinal areas. He found that the rapid growth causes frequent splitting of the ligament layers dorsal to the hinge line resulting in a weak, transversely thin ligament. A weak ligament is disadvantageous for burrowing because it only weakly resists shear stresses and resistance (Thomas 1976, p. 81). It may be concluded that Llandovery and Wenlock arcoideans were evolving from their infaunal ancestors towards a semi-infaunal, byssate life habit.

The dentition of *Uskardita* has clear affinities with that of *Alytodonta*. However, *Uskardita* has shorter pseudolaterals, and more numerous pseudocardinals that are perpendicular to the hinge line. This dental arrangement appears to be intermediate between *Alytodonta* and *Freja* and suggests that during the Wenlock, pseudocardinals began to cover most of the hinge plate (Text-fig. 7). This is of interest because the later arcids, cucullaeids and noetiids have dentitions that are dominated by small pseudocardinal teeth (Cox *et al.* 1969–71).

Two frejoid genera are known from the Upper Wenlock, and both can be readily derived from *Uskardita*. *Freja* has similarly arranged pseudocardinals, but displays a further modification to the pseudolaterals and the interumbonal duplivincular ligament. The ventrally diverging anterior and posterior pseudolaterals appear to have rotated so that they are almost parallel with the hinge line. The cardinal area and ligament have reduced in area, so that the umbones are less divergent and closer to the hinge. A reduced ligament may correspond with the small size of *Freja* (the majority of the specimens are less than 10 mm) and this may prevent comparison with *Uskardita*.

The phylogenetic position of *Trecanolia* is more difficult to determine. The genus is probably of similar late Wenlock age to *Freja*. The dental arrangements would suggest that *Trecanolia* is more derived from the ancestral arcoid (Text-fig. 7). In some specimens the pseudocardinal teeth have rotated to a ventrally convergent position which is typical of the arcids and noetiids. Furthermore, the more mature valves have denticles on the underside of the ventral pseudolateral teeth that resemble the pseudocardinals. This may mark a preliminary stage before the evolution of an entirely pseudocardinal dentition, as seen in the Jurassic arcoideans, but such a progression has hitherto not been recorded in the Upper Palaeozoic.

The origins of the later arcoidean families can only be tentatively suggested because of the limited material from the Palaeozoic. The Parallelodontidae may have evolved from a similar ancestor to the Frejidae (considered as a hypothetical parallelodontid/frejoid ancestor in Text-fig. 7). The elongate posterior pseudolaterals and ventrally convergent pseudocardinals could have originated from *Catamarcaia*, yet they have a ligament that is more closely related to the frejids. It is therefore proposed that a hypothetical ancestor gave rise to the Frejidae and Parallelodontidae during the mid to late Ordovician; this explains their rather similar cardinal areas and disparate dental arrangements.

The evolution of the Arcidae, Cucullaeidae and Noetiidae during the Mesozoic has been discussed by Stanley (1972, pp. 181–182, text-fig. 15). It was proposed that the parallelodontid subfamily Grammatodontinae arose from a late *Parallelodon* species in the Triassic, and that this subfamily was the ancestor of the family Arcidae. In turn, the families Cucullaeidae and Noetiidae

probably descended from the arcids during the Jurassic period (Stanley 1972). Papers that discuss post-Palaeozoic arcoid evolution include those by Stanley (1972) and Thomas (1976), and these should be referred to for further details.

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